COMMENTARY TO ACCOMPANY

The Metabolic Cost of Locomotion; Muscle by Muscle

In this issue of *Exercise and Sport Sciences Reviews* (*ESSR*), Umberger and Rubenson (1) explain and advocate for two new techniques that estimate the metabolic energy consumed by individual muscles during locomotion. These techniques (quantifying muscle blood flow using injectable microspheres and computer simulation of muscle mechanics/energetics) are providing insights unobtainable from measurements made at the whole-organism level. These techniques are important steps toward a comprehensive and more detailed understanding of the energetics of human walking and running in health and disease.

Since the 1890s, scientists have measured whole-body oxygen consumption rates for humans and other animals walking on treadmills. Such classic techniques are analogous to measuring the overall gas mileage of an automobile using the car's odometer and recording how many gallons it takes to refill the gas tank. If a driver notes that they need to fill up after covering fewer miles than usual, the obvious conclusion is that the car has developed a problem (perhaps a leaky fuel injector). To identify which cylinder has the problem, a mechanic would need to open the hood and measure the gasoline flow at each injector or attach a scanner to the car's computer port. The new tools presented by Umberger and Rubenson are allowing scientists to make analogous measurements on humans and other animals while they walk or run unencumbered. These tools can provide an accounting for when and how much metabolic energy is being consumed on a muscle-by-muscle basis.

These new tools are needed because unlike many other areas in physiology, there are no good animal models for the integrative process of human, bipedal locomotion. Standard laboratory animals, such as mice, rats, and dogs, are all quadrupedal. Our closest primate relatives (chimps, gorillas, and orangutans) are not skilled bipedal walkers or runners. Some birds are quite adept at bipedal gait, but unlike healthy humans, birds walk on their toes with their heels high in the air and with little movement at the hip joint. Thus, for studying locomotion, a hybrid approach, using nonhuman animals to validate computer models of human locomotion, can be a productive option.

However, these new tools come with their own sets of assumptions and limitations. Muscle blood flow seems to be well correlated with oxygen consumption, but the true rate of metabolic energy consumption varies with substrate usage (*i.e.*, the carbohydrate/fat fuel blend), and blood flow alone does not quantify substrate utilization. Furthermore, although blood flow measurements can approximate how much energy is consumed by specific muscles, it cannot identify which biomechanical task is consuming energy. This is because some individual muscles perform multiple tasks, and some muscles have actions at multiple joints. For example, the gastrocnemius muscle in humans contributes to body-weight support and forward propulsion of the whole body and also helps to launch the leg into the swing phase. In addition, the gastrocnemius has actions at the ankle and the knee, but one cannot deduce from blood flow which action is consuming energy. Computer simulations of gait have unveiled much about the biomechanics of locomotion at each joint and at each muscle. However, these simulations still rely on good old-fashioned electromyographic recordings for apportioning muscle forces, a process that itself is far from exact. Finally, even when the individual muscle mechanics are known, predicting the resulting metabolic energy consumption involves adapting models from *in vitro* muscle experiments on nonhuman animals.

Thus, if the goal is to reliably quantify the energy consumed by individual muscles in humans, we have a quandary. Direct measures of individual muscle-tendon forces and the work produced/absorbed have been obtained for running birds and other nonhuman mammals but are only possible for muscles with accessible, distinct tendons. Direct measurement of muscle-tendon force and work is too invasive for routine use in humans. Similarly, individual muscle blood flow measures using microspheres are not possible in humans because they involve sacrificing the animal to dissect and quantify the number of microspheres in each muscle. Essentially, we cannot measure muscle forces or energetics directly in humans, and we lack sophisticated computer models of nonhuman animal locomotion. Fortunately, computer simulations of the mechanics and muscle actions involved in nonhuman animal locomotion are in development. Such biomechanical

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models can then be validated using direct measurements of muscle-tendon forces and length changes. Validating these models for other species will improve computer simulations of human locomotion mechanics and increase our confidence therein. Furthermore, the validity of computer-simulated muscle energetics will be testable on nonhuman animals using microsphere-based muscle blood flow measures. A well-validated, integrative computer simulation of human gait energetics is probably a decade away, but as Umberger and Rubenson suggest, we are well on our way.

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Reference

1. Umberger BR, Rubenson J. Understanding Muscle Energetics in Locomotion: New Modeling and Experimental Approaches. *Exerc. Sport Sci. Rev.* 2011; 39(2):59–67.

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